THE DISPLACEMENT OF NATIVE ANT SPECIES BY THE INTRODUCED ARGENTINE ANT *IRIDOMYRMEX HUMILIS* MAYR*

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Introduction

Many authors have described how *Iridomyrmex humilis* Mayr has become a major pest throughout the world (Brun, 1924; Zimmerman, 1940; Smith, 1947; Morley, 1953; Skaife, 1961; Pasfield, 1968). Once these ants become established in a locality they will not tolerate the existence of any other species of ants, and as the populations of each colony build up in density, they emigrate in all directions, consolidating as they go and driving other species before them. Not only does *I. humilis* displace native ant species, but it has been shown to displace other introduced tramp species. The ant *Pheidole megacephala* F. is apparently a native to Africa and has been spread by commerce to almost all of the more humid parts of the world. It too is a serious pest and displaces native species. However, in 1852, in Funchal, the capital of Madiera, this species was itself displaced by *I. humilis* (Stoll, 1898; Wheeler, 1906). The displacement of *P. megacephala* by *I. humilis* has also been observed in the Hawaiian Islands (Wilson and Taylor, 1967; Fluker and Beardsley, 1970) and in Bermuda (Haskins and Haskins, 1965; Crowell, 1968). Wilson (1951) reports that a local naturalist in Mobile, Alabama observed *I. humilis* displacing the imported fire ant *Solenopsis saevissima richteri* Forel, and Fluker and Beardsley (1970) reported the displacement of *S. geminata* F. in Hawaii.

Shapley (1920 a, b) describes an "intermittent war" between *I. humilis* and the native California species which he feels would eventually eliminate most of the native ant species. Tulloch (1930) and Michener (1942) described the displacement of the California harvester ant *Pogonomyrmex californicus* by *I. humilis*.

Methods and Materials

In the present study, the displacement of three ant species, *P. californicus* Buckley, *Pheidole grallipes* Wheeler, and *Veromessor pergandei* Mayr, by *I. humilis* was observed for a six year period. Detailed observations of the displacement of *P. californicus* were

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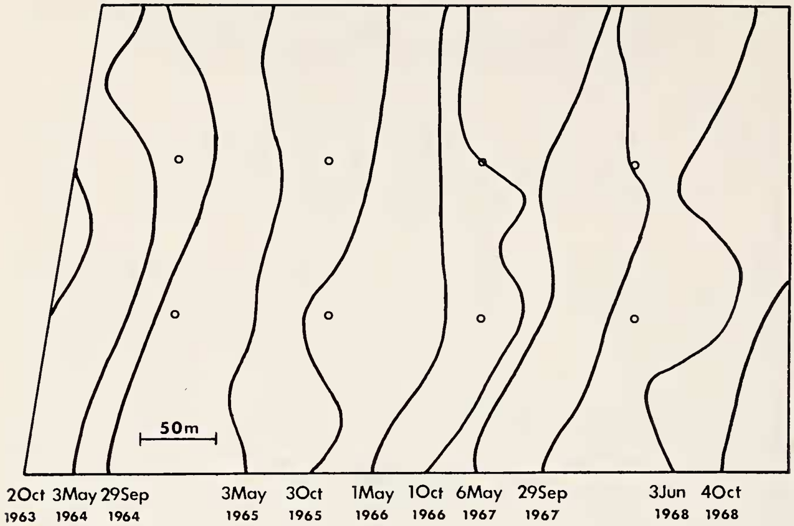

Figure 1. The forward advance of *I. humilis* as it displaces *P. californicus* in an old field from October 1963 to October 1968. Reference markers are located at intervals of 100 meters (o).

made at six month intervals, whereas only minor observations were made of the other two species. Studies were carried out in an old field from May 1963 to October 1968 in San Luis Rey, California, two miles east of Oceanside in San Diego County. The study field consisted primarily of sandy soil with *Bromus rubens*, *Salsola kali*, *Sonchus oleraceous*, *Heliotropium curassauicum*, and *Brassica nigra*, the dominant plants. The study area was almost rectangular, being 300 meters wide by 500 meters long on the south side and 450 meters long on the north side. The total area of the field was 14.25 hectares. The field was bordered by California Highway 78 on the west, dirt field roads on the east and south, and by a grass lawn on the north. Two additional fields of 5(2A) and 7(2B) hectares were located at the southern edge of the main study field. Here studies on colony size, foraging distance, and food preference were carried out (Erickson, 1972; and in manuscript).

All colonies of *P. californicus* and *I. humilis* were individually marked with color-coded wooden stakes placed one meter from the colony entrance. At intervals of approximately six months the position of each colony was noted on a large map, measured to the nearest one meter from the colony entrance using the reference

Table 1. The areas involved as *I. humilis* displaced native ant fauna in a southern California field.

Date	Total area occupied by *I. humilis* (m^2)	Total number of colonies in the whole field	Mean area per colony	Area added by *I. hum'lis* during time interval (m^2)	Number of colonies in the newly displaced area	Mean area per colony in newly displaced area (m^2)
2 Oct. 1963	390	2	—	390	2	195
3 May 1964	10608	7	1515	10218	6	1703
29 Sep. 1964	18926	15	1261	8318	6	1385
3 May 1965	34225	21	1629	15299	12	1275
3 Oct. 1965	48547	29	1674	14322	11	1302
1 May 1966	68535	35	1958	19988	14	1428
1 Oct. 1966	80593	29	2278**	12058	10	1206
6 May 1967	93396	36	2594	12803	9	1422
29 Sep. 1967	106166	42	2527	12770	8	1596
3 Jun. 1968	123654	47	2631	17488	12	1457
4 Oct. 1968	137699*	52	2648	13975	10	1398

*Does not include 4670m^2 in the southeast corner of the field still occupied by *P. californicus*. Total area involved therefore is 142,369 m^2 or 14.24 ha.

**Value obtained by subtracting 14531 m^2 underwater at the time of sampling from the total area involved.

markers placed at 100 meter intervals throughout the field (see Fig. 1). The lines on Fig. 1 deliniate the limit of eastward expansion of *I. humilis* colonies at the time the survey was taken. The new area added was then calculated by subtracting the total occupied area at the previous sampling date from the new total area occupied by *I. humilis.* This area was then divided by the number of colonies in the new added territory to get the mean area per colony values. At the same time, quadrat sampling with 30 randomly placed 2 meter by 2 meter quadrats were carried out to determine the vegetation characteristics. Weather data were taken from a station 3 miles northeast of the field site and averaged to get monthly mean temperatures and precipitation.

Results

The displacement of the three other ant species by *I. humilis* started slowly in October, 1963, but increased to an almost constant rate from 3 May 1964 to 4 October 1968 (Table 1, Fig. 1). The new area added by *I. humilis* during each displacement interval of six months was approximately 14000 m^2 ranging from 8318 m^2 to 19988 m^2 in the study field. The mean area per colony of *I. humilis* for the whole occupied portion of the field increased during each sampling interval, whereas the mean area per colony in the newly displaced land was almost a constant 1400 m^2 per colony. The number of colonies of *I. humilis* increased during each displacement interval as the displacement proceeded whereas the number of colonies of *P. californicus* decreased except for a minor fluctuation due to flooding between 3 October 1965 and 1 May 1966 (Fig. 2). By October 1968, not a single colony of *P. grallipes* was observed in the study field, and by 5 March 1969 all colonies of *P. californicus* and *V. pergandei* were located outside the boundaries of the study field. In their place remained 57 colonies of *I. humilis.*

Discussion

To explain this phenomenon of displacement, some comparison is necessary of the basic biology of the ant species involved. The nests of *I. humilis* are situated wherever there is sufficient moisture and where light is excluded, as under rocks and logs (Woodword, 1905, 1910; Eckert and Mallis, 1937, Smith, 1947) or in shallow nests in the soil (Cook, 1953). These ants occur in a wide variety of habitats — swamps, beaches, lawns and gardens, roadsides, houses, and various woodlands (Crowell, 1968). *I. humilis* are exceptionally restless ants and normally emigrate one or more times a season in search

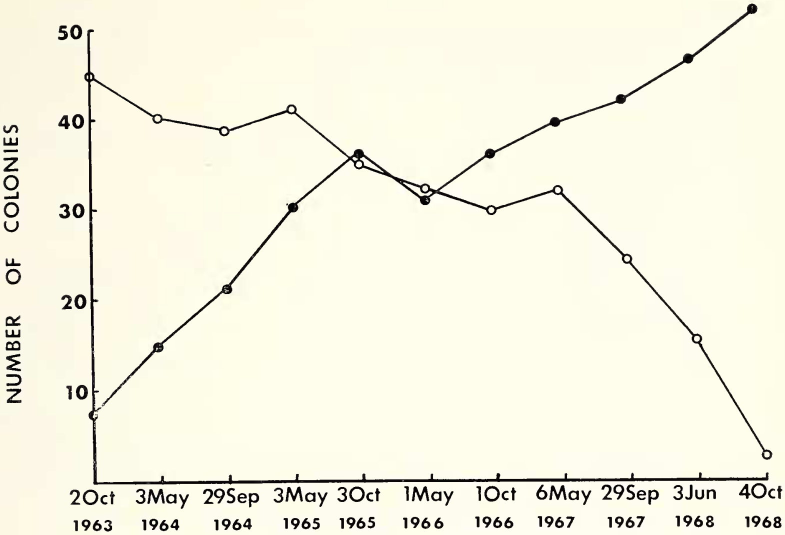

Figure 2. The number of colonies in the entire field of *P. californicus* (o) and *I. humilis* (•) from October 1963 to October 1968.

of more favorable habitats (Wilson, 1971). Colonies of *I. humilis* contain a large number of queens with thousands of workers (Smith, 1947) and proliferate by swarming of detachments of workers who accompany secondary queens out of the nest (Wheeler, 1933; Wynne-Edwards, 1963; Crowell, 1968). They are highly omnivorous but tend to seek sweet or fatty foods (Eckert and Mallis, 1937; Creighton, 1960; Cook, 1953), and tend aphids and scale insects in orchards and gardens (Skaife, 1961).

In contrast with *I. humilis*, the California harvesters are large ants (4-6 mm long) which are primarily seed gatherers, but are also known to be slightly omnivorous (Van Pelt, 1966). Colonies of *P. californicus* are small in comparison to *I. humilis* and contain only one queen. Proliferation takes place by large swarms of winged reproductives. The California harvester ant tends to nest in dryer semi-desert habitats and can tolerate much higher temperatures than *I. humilis* (Wheeler, 1926; Cole, 1932, 1968; Michener, 1942; Erickson, 1972).

The relative reproductive potential of *I. humilis* is probably much higher than *P. californicus*. This is most likely due to the large number of queens in each colony, the method of colony proliferation, and the omnivorous habits of these ants. These factors may also account for the great and rapid spread of *I. humilis* throughout the temperate regions of the world.

Basic differences in food resources limit to some extent the amount of competition between *I. humilis* and the three harvester ant species (Table 2). *I. humilis* is highly omnivorous whereas the three harvester ant species are only slightly omnivorous, being basically seed gatherers. *I. humilis* not only monopolizes the proven food sources but attempts to control the remaining foraging areas (Wilson, 1971). In the main study field, food, especially seeds, were very abundant. The food chambers of *P. californicus* and *I. humilis* were always full when the colonies were excavated. In fields 2A and 2B, the area was supplemented with approximately five pounds of mixed grass seed per month to determine the foraging characteristics and distances for *P. californicus.* The seeds, colored with common food coloring, were fully acceptable to the ants, making up 43 to 59% of the *P. californicus* food stores and 9 to 17% of the *I. humilis* food stores. The variously colored seeds were spread in concentric circles from a nest of *P. californicus* every 5 meters to a distance of 30 meters. The maximum foraging distance for *P. californicus* was about 10 meters except in areas where there was an *I. humilis* colony in which case the harvester ants foraged no farther than 5 meters even though the *I. humilis* colony was 20 meters away. Even though both fields were supplemented with a little over 50 pounds of mixed grass seed per year, in one year *P. californicus* was displaced 76 meters (2A) and 109 meters (2B) by *I. humilis.* It does not appear that this displacement is due to any overlap of a fundamental food dimension.

At each sampling interval the mean area per colony of *I. humilis* in the newly displaced territory was approximately 1400 m^2 whereas the mean area per colony for the entire field increased from 1400 m^2 to approximately 2600 m^2 during the five year period (Table 1). There thus appears to be a minimal area for a colony of *I. humilis* in the newly acquired areas and as these colonies become established and increase in population density, the colony requires a larger area.

Michener (1942) working with *P. californicus* encountered a similar displacement by *I. humilis.* He described in detail how individual harvester ants would be set upon and killed by groups of *I. humilis.* When temperatures are cool, *Pogonomyrmex* species tend to be sluggish and it is at this time that the Argentine ants torment the harvester ants as they forage around the nest (Michener, 1942).

Table 2. Food resources of *I. humilis* compared with species it has displaced throughout the world.

Species	Main Food Source	Degree of Omnivory	Reference
Iridomyrmex humilis Mayr	sweet or fatty foods, tends aphids scale insects, grains	+++	Wheeler, 1910 Eckert & Mallis, 1937 Creighton, 1950 Skaife, 1961
**Pogonomyrmex californicus* Buckley	seed gatherers	+	Wheeler, 1910 Forel, 1928 Wildermuth & Davis, 1931 Cook, 1953 Van Pelt, 1966 Cole, 1968
Pheidole megacephala F.	sweet or fatty foods	+++	Wheeler, 1910 Forel, 1928
**Pheidole grallipes* Wheeler	seed gatherers	+	Eckert & Mallis, 1937 Cook, 1953
**Veromessor pergandei* Mayr	seed gatherers	+	Eckert & Mallis, 1937 Cook, 1953
Solenopsis saevissima Forel	insects, fruits, grains, flowers, vegetables	+++	Creighton, 1950 Cook, 1953
Solenopsis geminata F.	insects, fruits, grains	++	Creighton, 1950 Fluker & Beardsley, 1970

*Displaced in present study.
+++ = highly omnivorous; ++ = moderately omnivorous; + = slightly omnivorous

Should a harvester ant come upon an Argentine ant during the warmer parts of the day, the former grasps the smaller ant with its mandibles and stings it to death (Michener, 1942). At dawn, sunset, or on a cloudy day the Argentine ants will attack and cling to the mandibles, legs, and antennae of the harvester ants and attempt to kill the larger ant. Observations made in the present study confirm Michener's discussion of the aggressive actions between the species.

There were no significant differences in the mean monthly temperature or precipitation from month to month (i.e. — all the Januarys, etc.) over the course of the study. The vegetation studies similarly showed that there was no significant difference in the order of dominance of the six plants mentioned. It does not appear that *P. californicus* ameliorates the habitat as it does not clear vegetation as many harvester ant species do. *I. humilis* does not utilize the same nest sites as the displaced species and in fact, not a single *I. humilis* colony was found within two meters of an abandoned harvester ant colony.

Pasfield (1968) found *I. humilis* displaced its neighbors at a maximum rate of 274 meters (300 yards) per year in Australia. This value is higher than the 100 to 200 meters per year at Fort Shafter on the island of Oahu between 1940 and 1944 (Pemberton, 1944) or the average of 100 meters per year in the present study (Fig. 1). Fluker and Beardsley (1970) observed *I. humilis* displace *P. megacephala* in Hawaii at about 66 to 100 meters per year. All these values seem low when compared to the displacement rate of 8 kilometers (5 miles) per year for native species by the fire ant *S. saevissima* in the Gulf states (Wilson and Brown, 1957).

The effectiveness of competition in nature is best demonstrated by the impact of an invading species on the native fauna. It appears that here, there is a tremendous competition for nest space, which is the general case for highly aggressive territorial ant species such as *Pheidole*, *Solenopsis*, and *Iridomyrmex* (Wilson, 1971). Three aspects of the populations biology of *I. humilis* gives this species a distinct competitive advantage over the native harvester ants. The general aggressive nature of *I. humilis* as well as the large number of queens and method of proliferation allow these ants to move in and establish new colonies in a very short time. Raiding columns of workers clear the way and pioneer groups of workers and queens follow into freshly opened nest areas.

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